



Spatial distribution and habitat assessment of *Panoquina errans* (Lepidoptera: Hesperiiidae) in San Diego County, California

KEITH GREER

San Diego Association of Governments, 401 B Street, Suite 800, San Diego, CA 92101

keith.greer@sandag.org

Abstract. *Panoquina errans* (Skinner, 1892), commonly known as the wandering skipper, is restricted to a narrow band of disjunct salt marsh habitat extending along the west coast of North America from Santa Barbara Co., California to the southern tip of Baja California, Mexico. A determination by the U.S. Fish and Wildlife Service of whether it represents an endangered or threatened species could not be made owing to a paucity of information on its biological vulnerability and threat. Based on a three-year survey (2010-2012) in San Diego Co., California, the species was observed in nine coastal lagoons and a coastal bluff. At all sites within the study area there was a significant correlation between the maximum annual observations of *P. errans* and the total area occupied by the larval host plant *Distichlis spicata* (Poaceae). The primary habitat for *P. errans* is coastal lagoons and coastal bluffs (100% of observations); elevations less than 5 m above mean sea level (98% of observations); within 25 m of patches of *D. spicata* over 1 m² (75% of observations); and containing *Frankenia*, *Cakile*, or *Heliotropium* (95% of observations).

Key Words: threatened and endangered species, salt marsh, California, Mexico, conservation.

INTRODUCTION

Panoquina errans (Skinner, 1892) occurs along the West Coast of North America from Santa Barbara County, California to the southern tip of Baja California Sur, Mexico (MacNeill, 1962; Donahue, 1975; Wells *et al.*, 1983; Faulkner & Klein, 2012). However, this wide distribution conceals the fact that it is restricted to a narrow band of disjunct coastal lagoon habitat that has diminished considerably over the last century. Although *P. errans* was considered a candidate for listing as endangered or threatened by the U.S. Fish and Wildlife Service (FWS) in 1994, it was determined that “persuasive data on biological vulnerability and threat are not currently available to support proposed rules” (FWS 1994).

Within San Diego County, populations appear to be small and stable throughout the coastal marshes

from Buena Vista Lagoon south to the U.S./Mexico border (Faulkner & Klein, 2012). The primary threat to the species has been the filling and/or dredging of coastal wetlands (Wells *et al.*, 1983), which is estimated to have been reduced by almost 88% in San Diego County (Oberbauer & Vanderwier, 1991; Zedler *et al.*, 2001). In addition to historical habitat loss, the threat of sea level rise, estimated to be between 12 and 61 cm by 2050 (National Academy of Science, 2012), may pose a significant future threat to this species (Reed, 1995; Zedler, 1996).

Little is known about the distribution, ecology, or population dynamics of the wandering skipper (FWS, 2008). In order to more effectively manage and conserve this species, I conducted investigations to define the current distribution of *P. errans* in San Diego County estuaries; define the key characteristics of occupied *P. errans* habitat at various spatial scales; and identify the commonly used nectar sources. These features were identified as critical uncertainties for the management of the species in San Diego County (FWS, 2008).

METHODS

Study Area. The study area included ten sites (nine coastal lagoons and one coastal bluff) in San Diego, California (Fig. 1). The region has a Mediterranean

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climate characterized by warm to hot, dry summers and mild to cool, wet winters (Dallman, 1998). San Diego's remaining coastal lagoons are small and discrete, confined to narrow river valleys separated by coastal hills (Zedler, 1982). The vegetation in these lagoons follows a vertical zonation from tidal creeks, through an intertidal zone of low to high marsh comprised of halophytic vegetation, to a transitional area of terrestrial vegetation (Penning & Callaway, 1992). Zedler (1982) characterizes the marshes as having low species richness, but showing a "wide variation in vegetation structure and functions from marsh to marsh, as well as within individual wetlands." The *P. errans* larval hostplant, *Distichlis spicata* (commonly referred to as saltgrass) (Well *et al.*, 1983; Brown, 1991), is a non-obligatory halophyte that can survive where the water table varies between 15 cm below and 5 cm above soil surface (Hansen *et al.*, 1976).

The nine lagoons included in this study run generally east to west from the ocean, have a range of hydrologic connectivity to the ocean, and are surrounded by a range of different land uses. These lagoons span the western edge of San Diego County, and were selected to confirm the occurrence of *P. errans* from historical reports and to survey appropriate habitat lacking information on the occurrence of the species. Access was limited to areas open to the public or where land managers gave permission for surveys to be conducted. Coastal bluffs were initially excluded from the study due to the perception of the low probability of occurrence from past literature, but an opportunistic sighting of an individual of *P. errans* on a coastal bluff suggested I should expand the survey area; one coastal bluff was included in the last year of the survey.

Field Surveys Protocols. The study was conducted from 2010-2012. During the first year, five lagoons (Table 1) were selected to determine the presence/absence of *P. errans* and determine its general distribution within the lagoons. The study began under the premise that habitat requirements of the wandering skipper were unknown (FWS, 2008), and therefore exploratory surveys were conducted in August and September of 2010. Survey methods generally followed those recommended by the FWS (2008) which state that they "should be conducted between 1000-1500 hours, when temperatures are between 65–90°F (18–32°C) and wind speed less than 10 mph (16 km/h)."

Surveys were conducted by two investigators. Each carried field binoculars, a camera, a net, and field guides (Emmel & Emmel, 1973; Bryant, 2010). The "checklisting" butterfly survey method described by Royer, Austin & Newton (1988) was used, walking

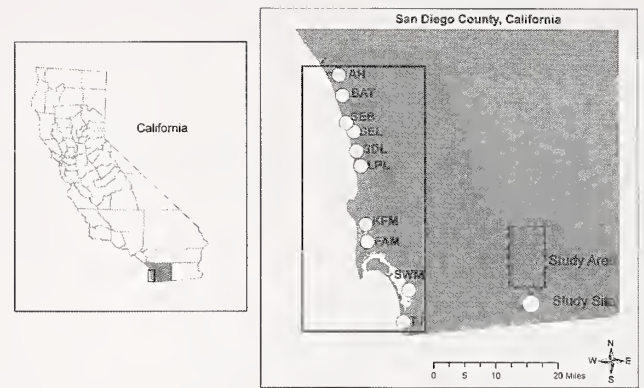


Figure 1. Location map of study area and study sites

a meandering transect through the lagoon until an individual skipper was observed. When an individual was discovered, the investigators walked in expanding concentric circles around the individual until no additional individuals were observed because progress was hindered by impassable tidal channels or terrestrial vegetation. This method allowed us to maximize the observation of individuals.

The second investigator was staggered approximately 10 m behind and 10 m to the left or right of the first. No active pursuit was made during the survey, and only individuals that were positively identified were recorded by the first investigator using a Trimble GeoExplore submeter accurate global positioning system (GPS). Observations from the second investigator were not counted unless subsequently observed by the first. The second investigator also kept track of individuals already counted that flew ahead of the first; these individuals were not recorded. The low height of the salt marsh vegetation allowed for excellent visibility, but tidal channels made some areas inaccessible. The average speed of the investigators was 12.1 m/min as tracked through the "routes" functions of the GPS. The results of the first year survey were downloaded into a Geographical Information System (GIS) running ArcGIS 10.1 to identify directional distribution polygons of skipper observations in the study area by generating one and two standard deviation ellipses around the observations (Mitchell, 2005). The average wind speed, humidity, temperature, and percent cloud cover were recorded prior to each survey using a Kestrel 3000 pocket weather meter. The elevation was obtained for each observation of *P. errans* from Lidar data from the National Oceanic and Atmospheric Administration (2012) with a minimum vertical accuracy of 9 cm.

Table 1. Survey information on study sites, year sampled, environmental conditions, detection dates, and extent of *Distichlis spicata* size mapped in the study site.

Study sites	Label	# of survey locations	Years sampled	Area (ha)	Total skippers observed	Max annual skippers	Avg wind (kph)	Avg hum %	Avg temp C ₁	Avg % cloud cover	Earliest detection date	Latest detection date	Sum of <i>Distichlis spicata</i> (m ²)
Agua Hendonia	AH	1	2011	0.6	11	11	3.6	68.4	22.4	0.0	8/31/2011	8/31/2011	175
Batiquitos	BAT	1	2012	1.44	43	43	3.4	68.1	21.0	30.0	7/2/2012	7/2/2012	219
Famosa Slough	FAM	2	2010-2011	1.86	167	108	4.6	72.9	22.8	24.0	7/29/2011	8/31/2011	1525
Kendall-Frost Marsh	KFM	2	2010,2011	4.33	2	2	3.0	73.7	24.4	22.0	8/27/2010	8/27/2010	10
Los Penasquitos Lagoon	LPL	3	2010-2012	19.1	121	86	4.6	68.5	25.5	22.5	7/14/2011	8/17/2010	1202
San Dieguito	SDL	2	2011	1.85	18	18	9.5	81.0	20.3	15.0	8/18/2011	8/18/2011	168
San Elijo	SEL	3	2010-2011	1.89	114	38	5.6	74.4	22.1	20.7	7/22/2011	8/31/2011	784
San Elijo Beach	SEB	1	2012	0.31	33	33	1.8	64.9	29.8	0.0	8/8/2012	8/8/2012	374
Sweetwater Marsh	SWM	3	2010-2011	4.41	29	15	9.7	72.3	23.5	0.0	8/3/2011	9/3/2010	780
Tijuana Estuary	TJ	3	2012	6.41	8	8	10.9	79.5	22.0	0.0	7/9/2012	8/7/2012	202
Total:	10	21		42.2	546								5439
Average:							5.7	72.4	23.4	13.4			543.9

During the second year, surveys for adults were conducted from 14 July 2011 through 31 August 2011 inside the two standard deviation ellipses generated from year 1. The surveyors utilized a Pollard walk methodology (Pollard, 1977; Pollard & Yates, 1993) within the ellipses along defined transect routes to maximize coverage within ellipses. Observed adults of *P. errans* and the plant species upon which they were nectaring and/or resting were recorded using GPS. The data were imported into GIS and was used to revise the standard deviation ellipses generated from the year 1 observations. For each revised ellipse, the mean center of the ellipse was calculated and a centerline bisecting the one standard deviation ellipse was established.

An assessment of the vegetation was conducted using systematic random sampling. Along the center line within the one standard deviation ellipse, a transect was laid out using a 100-meter field measuring tape. A point was selected at random within each 5-meter segment of the transect. A perpendicular transect was placed at the point extending between 10-25 m on each side of the transect and a point count was made for each plant species using a point intercept method (Elizinga *et al.*, 1998). Plant taxonomy followed the Jepson Manual (Baldwin *et al.*, 2012) as updated by the Jepson Flora Project (2012). The result was a grid of point counts of plant species within the one standard deviation ellipses that was used to characterize the area occupied by the adult wandering skippers.

In addition to transects, a series of plots based measurements were made to determine the percentage of plant species coverage (Elizinga *et al.*, 1998). A series of computer-generated random points were selected within the 1 standard deviation ellipses. A 1-m² plot was placed over a computer-generated random point, and abundance of plant species and percent cover estimates were collected using visual estimation. Two additional 1-m² plots were placed at 5 m from the center of the original plot at angles chosen at random between 1-180 degrees and 181-360 degrees of magnetic north. The result was an assessment area with a diameter of 10 m that included all three plots. If a skipper was observed at any time in the assessment area, the plots were considered occupied. The process was repeated until at least three groups of plots were measured that were recorded as occupied and three as unoccupied. While the transect data provides more information about each study site, the plot data allows for characterization of the vegetative cover of occupied and unoccupied areas within the study site. In addition to the transect and plot based vegetation surveys, a census of *Distichlis spicata* polygons greater than 1 m² with at least a 50% relative density (determined by visual estimation) was conducted within the one standard deviation ellipses that was used to characterize the area occupied by the adult wandering skippers.

In August 2011, two new lagoons were surveyed following the methods described above. While line transects were not conducted, plot assessments of the habitat were obtained and a census of *D. spicata* was done as described above.

The final year of surveys (2012) focused on expansion of the surveys, plot-based habitat assessments, and identification of *D. spicata* polygons into two additional lagoons that appeared to have suitable habitat and a third location where an opportunistic observation of a skipper occurred on a coastal bluff.

Data Analysis. A correlation analysis was conducted between the number of *P. errans* observed and the abundance of *D. spicata*, distance of individual to nearest *D. spicata* patch and open water, and elevation for each study site. Correlation coefficients and probabilities were determined using Spearman's rank correlation coefficient (r_s) due to the non-normality of some of the data (e.g., distance to *D. spicata* patch and open water appears to follow a Poisson distribution).

Multivariate analysis of the assemblage structure of plant species from transect data were conducted using non-metric multidimensional scaling (NMDS) (Mather, 1976) and a hierarchical, agglomerative cluster analysis using Primer-6 software (Clarke & Gorley, 2006) selecting group average methodology. Soerensen's distance measure of dissimilarity was used in both NMDS and cluster analysis. NMDS is a non-parametric approach to represent relationships between objects in multidimensional space using a matrix of ranked order of dissimilarity between objects (Quinn & Keough, 2002). Soerensen distance (also known as Bray-Curtis index when used for abundance data: McCune *et al.*, 2002) was selected because it ignores variables that have zeros for both objects; shared absences common in community studies do not affect the results (Field *et al.*, 1982; Faith *et al.*, 1987).

Transect data were standardized so that each site had a maximum total abundance of one (i.e., relative frequency to standardize for various study site sizes) and rare species, those that together contributed less than 10% of the overall abundance at a study site, were excluded to reduce noise in the data set without losing information (McCune *et al.*, 2002). An initial random start was selected in the ordination software to evaluate up to six axes to discern the usefulness of each. Stress values less than 10% were considered to represent a good ordination with no real risk of drawing false inferences as suggested by Clarke (1993). A similarity profile (SIMPROF) analysis was performed on the results of the cluster analysis to test for significance in structure of the clustered data using a significance level of 5% and Bray-Curtis similarity.

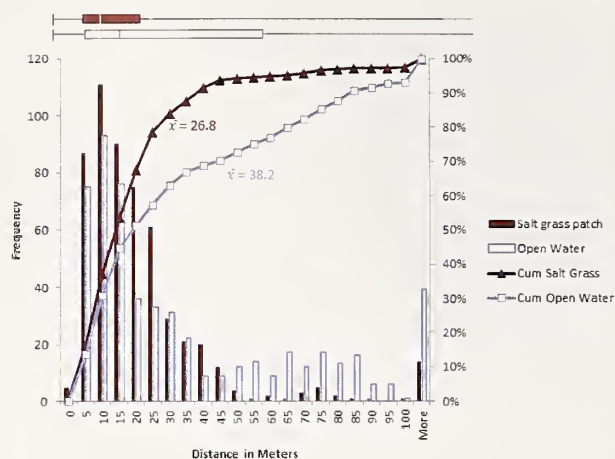


Figure 2. Frequency of *Perrans* observations compared to location of patches of *Distichlis spicata* (saltgrass) and open water. Bars represent frequencies in 5 m distance bins and line represents the cumulative number of skippers. Average is shown for all observed skippers (N= 546) from 2010-2012.

Data collected from plots were run through the same analysis structure (NMDS and cluster analysis) described above for the transect data. In addition, individual plots were grouped as occupied or unoccupied by skippers for the purposes of analysis. One-way Analysis of Similarity (ANOSIM) (Clarke 1993) was performed on the plots using the Primer-6 software to test for differences between group and community samples using a randomization test. Pairwise comparisons were summarized using global R (Clarke, 1993), a statistical measure that compares between-group to within-group dissimilarities. Monte Carlo permutation tests were used to determine statistical significance.

Data collected on the use of individual plants for nectaring and/or resting by skippers were evaluated among study sites and against the availability of that plant species at each study site using a two-tailed, paired Student's t-test ($n = 10$) after the data was arcsine transformed to account for utilization of relative frequency data.

RESULTS

Skipper Distribution. *Panoquina errans* was present in each of the nine lagoons surveyed and was also found on a coastal bluff (Table 1). Although well distributed throughout the study area, within each lagoon skippers were restricted to discrete areas of the study sites. Skippers were detected at all study sites during every

survey resulting in a high probability of detection, except for Los Penasquitos Lagoon (LPL3) were no skippers were observed during three visits to the site.

Across all study sites, skippers occurred on average within 26.8 m of *Distichlis spicata* patches and 38.2 m from the edge of open water (Fig. 2). A boxplot of distance of observed skippers to nearest recorded *D. spicata* patch indicates that over 75% (third quartile) of the observed skippers are within 25 m from *D. spicata* patches (Fig. 2). Distance to open water is more variable with the third quartile occurring at 55 m. The average elevation was 3.0 m above mean sea level (MSL) with a high of 6.5 m, a low of 1.7 m and a standard deviation of 0.67 m.

There was a strong ($r_s = 0.806$) and significant ($p = 0.005$) correlation between the maximum annual count of observed wandering skippers and the total area of *Distichlis spicata* in the study site (Table 2). Correlations between the count of skippers observed in the study sites and the average distance to nearest *D. spicata* patches, open water, and elevation were all negative, but weak ($r_s = -0.200, -0.127$ and -0.491 , respectively) and not significant ($p = 0.527, 0.687$, and 0.147 , respectively; Table 2).

Species composition and abundance. A total of 4868 individuals representing 66 plant species were recorded from transects ($n = 4250/60$ species) and plots ($n = 617/47$ species). Overall three species were responsible for 63% of the abundance in the study area: *Salicornia pacifica* (25.2%), *Frankenia salina* (23.3%) and *Distichlis spicata* (14.5%); however, variation did occur among study sites, especially at SEB which is discussed later. The majority of the plant species recorded ($n = 51$) contributed less than 10% to the overall abundance in the study sites. After standardizing and eliminating rare species, a total of 26 plant species of the 60 species remained from the transect data (Table 3). NMDS ordination recommended a 2-dimensional solution with a final stress of 5.3% after 35 iterations (Fig. 3a). Axis 1 and 2 cumulatively accounted for 93.2% of the variation. An analysis of outliers indicated that SEB was 2.14 standard deviations away from the average Soerensen distance of the other sites. All other sites were within 1 standard deviation. This result is not surprising given that SEB is a coastal bluff, whereas the other sites are within coastal lagoons. SEB does contain a significant abundance of *D. spicata* (32.6%), but has no *Frankenia* or *Salicornia*. In addition, SEB has a high percentage of non-native plant species (59.5%). The cluster analysis of transect data showed a weak structure with SEB being the only significantly distinct cluster ($p = 0.04$) compared to the other study sites); there was no significant difference between the lagoon study sites.

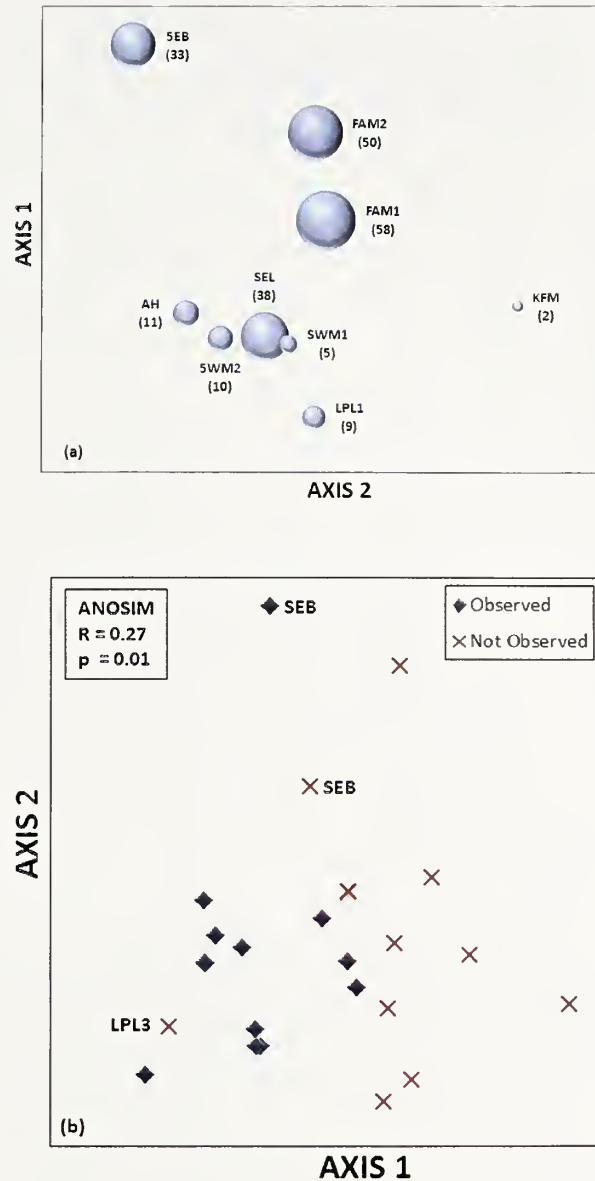


Figure 3. Results of non-metric multidimensional scaling (NMDS) on vegetation data collected from transects and plots. (a) NMDS labeled by study site on transect data. Area of symbols represents size of maximum annual observations (shown in parentheses) next to study site label. (b) NMDS by study sites on plot data. ANOSIM score of plots where skippers were observed and not observed displayed with probability of occurring by chance alone.

Data collected from the plots were run through NMDS to evaluate the assemblage structure of plant species in plots that contained adult skippers and those that did not. NMDS ordination on the plot data recommended a 3-dimensional solution with a final stress of 8.2% after 202 iterations (Fig. 3b). Axis 1, 2 and 3 cumulatively accounted for 92.7% of the variation. Figure 3b shows the ordination

Table 2. Maximum of annual skippers observed by study site compared to environmental covariates. Results of Spearman's rank correlation regression analysis and probably of occurring by chance alone are shown. Bold italics indicate significance at ($\alpha = 0.05$).

Study Site	Max annual skippers observed	Sum <i>Distichlis spicata</i> (m ²)	Average distance to <i>Distichlis spicata</i> (m ²)	Average distance to open water (m ²)	Average elevation m above MSL
AH	11	175.0	91.1	8.1	3.0
BAT	43	219.0	16.6	13.1	2.6
FAM	108	1525.0	10.7	19.8	2.5
KFM	2	10.0	3.8	15.6	2.9
LPL	86	1202.0	56.0	24.0	2.8
SDL	18	168.0	15.9	22.9	3.8
SEL	38	784.0	36.7	14.0	3.9
SEB	33	374.0	77.3	8.1	3.0
SWM	15	780.0	104.1	133.5	2.9
TJ	8	202.0	68.7	202.1	3.1
r_s		<i>0.806</i>	-0.200	-0.127	-0.491
p		<i>0.005</i>	0.527	0.687	0.147

with plots occupied by skippers and plots not occupied by each study site. An ANOSIM indicated a significant difference between those plots identified as unoccupied and occupied (global $R = 0.27$; $p = 0.01$). The cluster analysis resulted in a clear distinction between the coastal bluff site, San Elijo Beach (SEB), from the lagoon plots ($p = 0.03$), but was not distinct ($p = 0.07$) from areas within SEB identified as occupied and not occupied. Plots located in coastal lagoons identified as not occupied by skippers were distinct ($p = 0.001$) from those that are occupied. Los Penasquitos 3 (LPL 3) was the outlier ($p = 0.009$), clustering distinct from all other groups, but more closely related to plots identified as occupied even though no skippers were observed.

Nectaring and Resting. Of the 546 observations of wandering skipper, nectaring or resting was observed on only eight plant species, and 97.6% of all sightings occurred on just three species (*Frankenia salina*, *Distichlis spicata* and *Cakile maritima*; Table 4). While 3.5% of the observations were on *D. spicata*, this is assumed to be "resting" because grass species have no nectar. In the lagoons, *Frankenia* by far was the most commonly used species. Along the coastal bluff site at SEB, *Frankenia* was absent and the

skippers were observed on *Cakile* and *Heliotropium*. Among all study sites, *Frankenia* was used significantly more than expected by chance when compared to abundance of other plant species within the study area ($p < 0.001$), whereas *Distichlis spicata* and *Salicornia* were significantly under-used compared to their abundance in the study sites ($p = 0.019$ and $p = 0.0009$, respectively). The other five plant species upon which wandering skippers were observed were not utilized significantly different ($p \gg 0.05$) compared to their abundance within the study sites (Table 4).

SIMPER Analysis. When the plots were grouped as occupied or unoccupied by skippers, the overall average vegetation dissimilarity among the groups was 68.18%. *Frankenia* was three times as abundant in occupied sites as unoccupied, while *Salicornia pacifica* was twice as likely in unoccupied sites as occupied. *Distichlis spicata* was equally likely to occur in either group. The abundance of these three species alone contributed 92.63% of the similarity between study sites identified as occupied and 87.24% between study sites identified as unoccupied. Los Penasquitos Lagoon 3 (LPL3) was kept with the unoccupied group for this analysis because it represents a single albeit unique sample.

Because SEB was a coastal bluff site that lacked lagoon vegetation, it was separated into a third group. Separating SEB, did not significantly change the average dissimilarity between lagoon groups identified as occupied and unoccupied (63.73%), but the average dissimilarity of SEB was greater than 92% compared to group 1 (occupied) and 93% compared to group 2 (unoccupied). *Cakile maritima*, *Distichlis spicata* and *Carpobrotus edulis* were the three key contributors to the coastal bluff site which lacked *Frankenia salina* and *Salicornia pacifica*. Among all three groups of plots, *Distichlis spicata* was always present and contributed between 10 to 14% of average abundance.

DISCUSSION

Distribution. *Panoquina errans* was found in each of the lagoons and the one coastal bluff surveyed. Within all study sites, however, skippers were clumped in their distributions. The abundance of skippers varied among sites independently of the size of the sites. A low of two skippers were observed at the 4.6 ha Kendal Frost Marsh (KFM), and a high of over >150 individuals were recorded at the 1.86 ha Famosa Slough (FAM).

The nine lagoons likely cover the full range of potential habitat in San Diego County. Two lagoons, San Luis Rey and Buena Vista, were excluded from the study due to their very limited tidal habitat.

The chance observation and subsequent survey of a population of skippers along a coastal bluff maybe the most interesting aspect of this study, and corroborates an observation by Orsak (1977) of a skipper in heavily disturbed coastal bluffs. Subsequent reconnaissance surveys in the summer of 2013 (not included in this analysis) have confirmed additional observations along coastal bluffs in Carlsbad, California (between study sites AH and BAT), and along Del Mar to the north of LPL. Preliminary genetic data suggests that the coastal bluffs may serve to connect the coastal lagoon populations and help maintain gene flow (Daniel Marschalek, pers. comm.).

This study could not confirm a previous hypothesis (Zedler, 1982) that the largest population in the United States exists at the Tijuana Estuary (TJ). I found skippers in multiple locations in TJ at low abundance; however, the largest area of *Distichlis spicata* observed in the entire study area (over 1.5 ha) occurs along the northern arm of Oneonta Slough. This area was restricted from surveys due to the breeding season of endangered birds, but holds promise for an abundant number of wandering skippers.

Key Characteristics of Habitat. All survey sites contained *Distichlis spicata*, but they were not necessarily dominated by *D. spicata* (average 14% cover with a range from 0–30%). More significant was the size of the *D. spicata* patches within study sites. For example, small areas of *D. spicata* (10 m²) were observed at KFM, a site that yielded only two sightings of *P. errans*. In contrast, FAM had 1525 m² of *D. spicata* where 108 skippers were observed. Also of note was that 75% of skipper observations were recorded within 25 m of a *D. spicata* patch greater than 1 m².

The habitat characteristics within the lagoon and along the coastal bluffs are distinct as discussed in the results of the cluster analysis and should be separated for identification of key characteristics that make up the habitat. The lagoon sites where skippers were observed contain an abundance of native plant species and are not significantly different in their composition. Across all study sites *Frankenia*, *Salicornia* and *Distichlis spicata* dominate the lagoon study sites with an abundance of 63% of the total plant cover recorded. The majority of species richness in the lagoon sites (51 species) comprises less than 10% of the abundance. Among study sites, 46 species (70%) occurred at less than 4 of the 9 lagoon study sites. This is consistent with Zedler's observation (1982) of the marshes lacking species richness, but showing a wide variation in vegetation from marsh to marsh.

Of interest is the negative association of skippers with *Salicornia*. This halophytic species typically occurs in the low to mid-elevations of the marsh, sometimes forming monotypic stands. This negative association supports the hypothesis that the low marsh areas dominated by *Salicornia* are not key habitat areas.

LPL3 stands as an outlier among the lagoon study sites. Three areas of Los Penasquitos Lagoon study site were examined, the first two contained skippers, the third did not. LPL3 is characterized by an assemblage of plant species similar to those occupied by wandering skipper as demonstrated with the NMDS analysis. *Frankenia* covers half the LPL3 plots with a large area of *Distichlis spicata* (400 m²) and open water within 15 m. The difference is that LPL3 is 2.3 km away from the tidal water at an elevation between 7.7 and 8.0 m above MSL. This area is never inundated by tidal waters and is best described as an alkali marsh rather than a salt marsh lagoon. In this study all observation of skippers occurred at elevations less than 7 m above MSL. This may be an important diagnostic indicator.

The one coastal bluff site was dominated by non-native plant species (58.5%). The dominant native species was *Distichlis spicata* (32%) with other native species contributing less than 2% cumulatively. *Cakile maritima* and to a lesser extent *Heliotropium curassavicum* were the dominant flowering plants where skippers were observed. Non-native weedy species such as *Carpobrotus edulis* (20.1%), *Myoporum laetum* (9.3%) and *Cortaderia jubata* (5.6%) were some of the key dominant species on the coastal bluff. Not surprisingly, *Frankenia* and *Salicornia* (species closely tied with coastal lagoons) were absent from the coastal bluff.

Nectar/Resting. This study did not determine the difference in plants being used for food (nectar) and those that were used for resting. Even so, the majority of skippers in the coastal lagoons were observed on *Frankenia* (85.2%). Compared to the availability within the study area, this plant species was used significantly more than by chance alone ($p = 0.0003$). *Frankenia* represents a key nectar source in the lagoon study sites. There seems to be a negative association with *Salicornia* and *Distichlis spicata*. This can be attributed to the lack of nectar available from these species. The only outlier was the BAT site for which skippers were observed 16% of the time using *D. spicata* compared to the 7% of available habitat.

On the coastal bluff, the skipper's ability to switch from *Frankenia* to *Cakile* and *Heliotropium* demonstrates the skipper's flexibility in use of nectar sources. Whereas other authors (Orsak, 1977; Busnardo, 1989; Brown, 1991) reported deerweed (*Acmispon*

Table 3. Species together contributing $\geq 90\%$ of total abundance at each study site. All data are from transects, except BAT, LPL3 and TJ which are from plot data and shown for illustrative purposes. Transect and plot data were separated for cluster and NMDS analysis. Species shown in red italics are non-native species.

	AH	FAM1	FAM2	KFM	LPL1	LPL2	SEB	SEL	SWM1	SWM2	BAT*	LPL3*	TJ*
<i>Frankenia salina</i>	28.0	11.3	7.8	5.8	30.4	17.6		40.4	37.3	38.9	30.6	50.0	43.5
<i>Sarcocornia pacifica</i>	17.2	22.0	7.3	22.7	23.5	36.5		36.4	19.0	15.2	33.7		
<i>Distichlis spicata</i>	16.1	31.2	34.2			18.5	32.6	6.5	9.0	12.1		3.3	21.0
<i>Distichlis littoralis</i>		6.6		42.5					16.0	2.0			
<i>Lollum multiflorum</i>					39.1								
<i>Batis maritima</i>		8.9		15.2						3.5			
<i>Jaumea carnosa</i>		6.3	15.0					3.0					
<i>Carpobrotus edulis</i>						3.2	20.2						
<i>Helminthatea echoides</i>	21.5												
<i>Arthrocnemum subterminale</i>			4.7			2.8			4.2	9.1			27.4
<i>Cuscuta salina</i>		3.9	7.3			4.3		4.0					
<i>Cakile maritima</i>							15.9						
<i>Cressa truxillensis</i>	3.2								4.8	3.0	4.6		
<i>Myoporum laetum</i>							9.7						
<i>Cortaderia jubata</i>							5.8						
<i>Limonium californicum</i>				5.8									
<i>Avena barbata</i>			5.2							5.1			
<i>Bromus hordeaceus</i>													
<i>Isocoma menziesii</i>						4.8							
<i>Bolboschoenus maritimus</i>			4.7										
<i>Juncus arcticus ssp. littoralis</i>	4.3												
<i>Juncus acutus</i>			4.1										
<i>Acacia sp.</i>							3.5						
<i>Arundo donax</i>							3.5						
<i>Atriplex semibaccata</i>										2.5		10.7	
<i>Spartina foliosa</i>											14.4		
<i>Artemisia palmeri</i>											7.6		
<i>Cyperus eragrotis</i>												10.7	
<i>Artemisia californica</i>												6.6	
<i>Salix gooddingii</i>												6.6	
<i>Malvella leprosa</i>												4.1	

Table 3 (Cont.).

	AH	FAM1	FAM2	KFM	LPL1	LPL2	SEB	SEL	SWM1	SWM2	BAT*	LPL3*	TJ*
<i>Ambrosia psilostachya</i>						2.4							
Total	90.3	90.3	90.2	92.0	93.0	90.1	91.1	90.2	90.2	91.4	90.9	92.0	91.9

bold italic = non-native species

Table 4. Utilization of specific plant species for nectaring and/or resting by study site for all observed skipper in the study (n = 546). The percentage of plant species used (observed) by wandering skippers is compared to the total abundance of that plant species occurring in the study site was tested using a two-tailed, paired Student's t-test. Percentage data was arcsine transformed prior to running the t-test. Probability of occurring by chance alone is shown. **Bold italics** are significant at $\alpha = 0.05$.

Study site	<i>Frankenia salina</i>		<i>Distichlis spicata</i>		<i>Callitriche maritima</i>		<i>Heliotropium curassavicum</i>		<i>Miscanthus sinensis</i>		<i>Carpobrotus edulis</i>		<i>Arthrocnemum subterminale</i>		<i>Salicornia pacifica</i>	
	Observed	Available	Observed	Available	Observed	Available	Observed	Available	Observed	Available	Observed	Available	Observed	Available	Observed	Available
AH	91%	27%	0%	13%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	19%
BAT	84%	21%	16%	7%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	21%
FAM	100%	11%	0%	29%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	16%
KFM	100%	5%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	23%
LPL	94%	19%	4%	17%	0%	0%	0%	1%	0%	0%	0%	0%	0%	0%	2%	34%
SDL	94%	25%	6%	10%	0%	0%	0%	0%	0%	0%	0%	3%	0%	0%	4%	14%
SEL	96%	39%	4%	7%	0%	1%	0%	0%	0%	0%	0%	0%	0%	0%	0%	36%
SEB	0%	0%	3%	32%	73%	16%	21%	0%	0%	0%	0%	19%	0%	0%	0%	0%
SWM	93%	35%	0%	10%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	6%	17%
TJ	100%	20%	0%	30%	0%	10%	0%	0%	0%	0%	0%	0%	0%	0%	20%	0%
Average	85.2%	20.3%	3.3%	15.5%	7.3%	2.7%	2.2%	0.3%	0.7%	0.3%	0.3%	2.6%	0.9%	3.5%	0.2%	17.9%
p=	0.0003	0.01911	0.45353	0.41604	0.18901	0.28672	0.34344	0.18901	0.28672	0.00089						

glaber), salty susan (*Jaumea carnosa*), chrysanthemum (*Chrysanthemum coronarium*) and goldenbush (*Isocoma*) as nectar sources, these were not documented in the present study. *Jaumea* was present in 7 of the 9 lagoon study sites, but skippers were never observed utilizing it. *Acmispon* and *Isocoma* are present along the transitional fringe of the lagoon, and despite extra effort to confirm the use of these plants, no skippers were observed nectaring on these. *Chrysanthemum* was not recorded from any of the study sites. *Frankenia*, *Cakile* and *Heliotropium* are the key nectar sources for wandering skippers, but the data suggest that the species may be opportunistic in regards to nectar source utilization.

A Conceptual Model. Based upon work done in this study, the author would like to offer a conceptual model for the habitat of wandering skippers. The primary habitat for wandering skippers consists of coastal lagoons and coastal bluffs (100%); elevations less than 5 m (98%); within 25 m of patches of *Distichlis spicata* over 1 m² (75%); and containing *Frankenia*, *Cakile* or *Heliotropium* (95%).

CONCLUSIONS

P. errans were found throughout San Diego in discrete areas of coastal lagoons and coastal bluffs. This study supports the observation that wandering skippers are not restricted to tidelands and estuarine habitat, and can occur along coastal bluffs. This study does not support the conclusion that the wandering skipper is dependent upon *Distichlis spicata* that is at least wetted by high tides (Nagano *et al.*, 1981), since observations of skippers using coastal bluffs were well above even the highest tides and storm surge. Conversely, skippers were not observed in what appeared to be suitable but unoccupied habitat (i.e., LPL3) well away from tidal influence. This study supports the hypothesis by Busnardo (1989) that the skippers favor lower and wetter, rather than drier areas of the salt marsh, but not areas of monotypic *Salicornia*.

This study lacked the ability to look at soil salinity or the potential physiological aspects of salt on the skippers, but the proximity to either tidal channels or salt spray from the ocean waves appear to influence the skipper's distribution. *Distichlis spicata* distance and the total amount present are important in the presence of the skipper and its abundance. While others have observed wandering skippers utilizing several species of plants for nectaring, this study concluded that 95% of the nectaring or resting occurred on just three species (*Frankenia*, *Cakile* or *Heliotropium*).

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